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Abundance Modeling and Movement of smallmouth bass in a Regulated Section of the Broad River, SC

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ABUNDANCE MODELING AND MOVEMENT OF SMALLMOUTH BASS IN A REGULATED SECTION OF THE BROAD RIVER, SC

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Seth Mycko
August 2017

Accepted by:
Dr. Yoichiro Kanno, Committee Chair
Dr. Patrick Jodice
Mr. Jason Bettinger
ABSTRACT

Dams and altered flow regimes impact riverine fish. In addition to ecological impacts, unpredictable changes in flow influence the ability to access rivers and effectively sample fish populations. Fisheries management practices are often influenced by water regulation and hydropower generation, thus designing distinct methods of monitoring populations in regulated rivers is critical for effective management. Recurrent changes in river flow also influence behavior of fish inhabiting the flow-regulated portions of rivers, and such individual behavior may ultimately have population-level effects (e.g. fish abundance).

I investigated population abundance and movement of smallmouth bass (*Micropterus dolomieu*) within a regulated portion of the Broad River, SC, located below a small hydropower dam. In Chapter 1, I developed a novel approach to estimating bass abundance within a 4.2-km section immediately below the dam where fluctuations in discharge might influence capture efficiency over different sampling days. The number of smallmouth bass was estimated based on mark-recapture data utilizing two gears, angling and electrofishing. The closed population assumption was confirmed using radio telemetry, and closed population capture-mark-recapture models were fit in the Bayesian hierarchical modelling framework with an estimated number of 2,380 bass (95% Credible Interval: 1,578-3,693) over 200 mm TL. Integrating the two gear types into a mark-recapture study can be an effective method for assessing abundance in spatially or temporally heterogeneous habitats where changing conditions can cause variable sampling environments.
In Chapter 2, to inform the sampling strategy to detect a temporal trend in bass abundance, I implemented a power analysis comparing the ability to detect a 2.5% or 5% annual declining trend in abundance after 5, 10, and 15 years based on various levels of sampling effort. The primary interest was to optimize the allocation of effort in terms of number of survey occasions within a year and intensity of effort for each survey occasion. Results indicated that increased effort intensity of each survey occasion (e.g. more boats to be used on each survey to increase capture probability) was more important than adding more occasions with lower effort/bass detection levels within each. In general, power increased with the larger decline (5%) and more sampling effort.

In the third and final chapter, I evaluated the effects of river discharge variation on diurnal fish movement every 30 minutes during daylight hours to establish linkage between hydro-power generation and fish behavior. Generalized additive mixed models (GAMMs) suggested that movement distances slightly increased with river discharge associated with hydro-power generation in winter, but not in summer. The physiological impacts of this altered behavior was not known, but if rapid and major changes in flow magnitude act as a stressor to individual bass, then population-level effects could follow and impact fisheries resources within the study area.
ACKNOWLEDGMENTS

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CHAPTER ONE

Using angling and electrofishing to estimate smallmouth bass abundance in a regulated river

Introduction

Abundance estimation is a fundamental aspect of fisheries management. Sufficient knowledge of fish population size is critical to informing management decisions such as length limits and stocking rates. Assessment of abundance is accomplished through various methods. Catch per unit effort (CPUE) from standardized sampling is commonly used (Copeland, Orth, & Palmer 2006; Balcombe & Arthington 2009). Depletion and removal techniques are often employed by blocking off a habitat section in streams (Rosenberger & Dunham 2005; Habera, Kulp, Moore, & Henry 2010) and rivers (Odenkirk & Smith 2005). Mark-recapture methods exist for abundance estimation in closed-populations (i.e. no births, deaths, immigration or emigration). The two-sample Lincoln-Petersen and multiple-sample Schnabel methods require batch mark data over a short period to satisfy population closure (Modde, Burnham, & Wick 1996). Mark-recapture data of unique individuals provide the richest data for estimating abundance of a closed population because they record individual capture histories over sampling occasions (Pine et al. 2003).

Despite the availability of various methods, abundance estimation is complicated in flow-regulated rivers due to their large size and fluctuating discharge (i.e. spatial and temporal heterogeneity). Multiple gears are often used to sample populations and assemblages across many different lentic (Weaver, Magnuson, & Clayton 1993; Jackson
& Harvey 1997; Rogers, Hansen, & Beard 2005; Ruetz, Uzarski, Krueger, & Rutherford 2007) and lotic (Arab, Wildhaber, Wikle, & Gentry 2008; Pregler, Vokoun, Jensen, & Hagstrom 2015) habitat types in a single sampling location. Flow regulation can produce different sampling environments subject to rapid changes in discharge. Changes in flow condition could prevent the use of a single gear even within the same habitat types on different days (Casselman, et al. 1990). Spatial and temporal heterogeneity of regulated rivers necessitates a creative approach to combining sampling methods to estimate abundance.

There is a lack of information available on how data from multiple gears could be combined to inform abundance estimation. Gears have inherent sampling biases (Beamsderfer & Rieman 1988) and abundance estimation is further complicated by variable sampling efficiency resulting from spatial and temporal heterogeneity in rivers. Thus, CPUE, a common method for assessing abundance, cannot be applied reliably because it measures the product of true abundance and capture probability. Changes in CPUE can result solely from varying capture probability due to sampling conditions. Mark-recapture surveys require several days of sampling and capture efficiency may be affected by varying discharge conditions during the sample period. Characterizing this temporal variation in capture efficiency should result in more accurate abundance estimates, which may be accomplished through the integration of multiple gear types.

Abundance estimation in regulated rivers is a global challenge. Dams and other water control structures have been constructed extensively in rivers (Dynesius & Nilsson 1994), and additional projects are proposed in many parts of the world (Grill et al. 2015).
Although dams affect native lotic fishes (Jager et al. 1997; Osmundson, Ryel, Lamarra, & Pitlick 2002; Murchie et al. 2008), regulated rivers still provide recreational angling opportunities for a number of species. Thus, maintaining fisheries as well as other recreational river uses should be among the major management objectives for flow-regulated rivers (Babel, Gupta, & Nayak 2005).

In this study, abundance of smallmouth bass, *Micropterus dolomieu* L., was estimated in a 4.2 km section of the Broad River, a flow-regulated river located in South Carolina, USA, using a mark-recapture method. Angling and boat electrofishing were used on different sampling days to correspond to fluctuating river discharge conditions characteristic of a flow-regulated river. Imperfect and variable capture of individuals was addressed in a Bayesian state-space model. Simulations were used to explore the behavior of these abundance models integrating two different gears that likely had differing sampling biases, and the key assumption of population closure was validated utilizing radio telemetry to monitor bass movement.

**Methods**

*Study area*

This study was conducted in the Broad River (South Carolina, USA) between the Ninety-Nine Islands and Lockhart dams (Fig. 1-1). Abundance sampling was performed in the 4.2 km section immediately below the Ninety-Nine Islands Hydroelectric Station, but telemetry efforts were expanded to include the 13.4 km portion of the river to maximize the chance of detecting any potential emigration from the 4.2 km abundance section. The
river has a total drainage area of 9,819 km\(^2\), and flows approximately 240 km through the lower Blue Ridge and northern Piedmont regions of North and South Carolina. Lotic habitats consist primarily of larger boulders, cobble/gravel riffles, and scoured sandy pools. Large shoals coupled with temporally variable discharge create difficult sampling situations. River discharge is variable and regulated via several run-of-the-river dams. During the last 15 years, mean annual discharge ranged between 774 – 4200 ft\(^3\)/s (USGS Gage 02153551). Surrounding land use is dominated by pasture lands with mixed forest and a few industrial complexes.

Smallmouth bass (hereafter ‘bass’) are a recreationally important game fish native to the Ohio/Mississippi River and Ozark mountain drainages. These bass have been introduced outside of the native range to improve fishing opportunities (Brewer & Orth 2015). Monitoring the size and trend of both native and non-native bass populations is an important management objective throughout the USA, in order to infer predation impacts on native fish populations (Fritts & Pearson 2004) and justify stocking resources (Buynak, Kornman, & Surmont 1991; Weidel, Josephson, & Kraft 2007). Within the Broad River, smallmouth bass have been stocked since 1984 to enhance recreational fishing opportunities and natural reproduction does occur in the river (Bettinger 2013).

*Mark-recapture sampling*

A mark-recapture survey was conducted on five days (hereafter ‘occasions’) between October 20 and November 11, 2015. Sampling was completed over 22 days to conform to the population closure assumption. Two gear types were chosen due to
fluctuations in river discharge during the study. At lower discharges (<1,500 ft$^3$/s), boat electrofishing is difficult as many shallow areas of the river are inaccessible with motor boats. During periods of higher discharge (>1,500 ft$^3$/s), angling is ineffective because of swift currents. Angling was utilized during the first two occasions when 11 anglers floated downstream from the Ninety-Nine Islands dam in kayaks and canoes (Fig. 1-1). Anglers were supplied with and instructed to use at least one of three lures (in-line spinners, jigged grubs, and soft plastic minnows). Anglers got out of their kayaks or canoes at shallow shoals to wade and sample the entire width of the channel. All captured bass were held in livewells or soft mesh bags, and transported to the closer of two tagging teams. To minimize handling time and stress, bass were tagged and released as quickly as possible. The small, light (<4 g) lures used for angling were best suited for shallower, slower flowing, habitats. Deeper pools and fast flowing riffles were sampled less intensively in order to spend additional time in shallower runs with higher capture potential.

Electrofishing was conducted during higher flow conditions (>1,500 ft$^3$/s) when anglers could not wade safely. A single boat equipped with a Smith-Root GPP 2.5 electrofisher (Smith-Root Inc., Vancouver, WA) was used during three subsequent sampling occasions working downstream from the upper extent of the study section. The sample section was divided into four sub-sections using three large shoal areas as breaks where sampling was stopped and captured bass were transferred to another boat for measuring total length [TL in mm] and tagging. After handling, the bass were released at the mid-point of each sub-section.
All bass >100 mm TL were held in an aerated livewell of river water until an 8 mm passive integrated transponder (PIT) tag (Oregon RFID Inc., Portland, Oregon) was injected intracoelomically using a Biomark MK165 implanter and N165 needle. Tags were implanted ventrally approximately 20 mm posterior to the pelvic girdle (Roussel, Haro, & Cunjak 2000). To aid in the identification of recaptured bass, the left pectoral fin was also clipped on all bass after their initial capture. All recaptured bass were measured, scanned for a tag number using either an Avid Identification Systems Power Tracker (Avid Identification Systems Inc., Norco, California) or Oregon RFID Easy Tracer II scanner. The tag number was then recorded, and the bass were promptly released.

**Abundance Modeling**

Capture-recapture data were analyzed using Bayesian state-space models (Kéry and Schaub 2012). Capture histories of all individuals \( i \) across sampling occasions \( j \) were created as a two-dimensional array, \( y_{i,j} \), where 1’s represent captures and 0’s non-captures. Of the bass that were tagged, eight suffered excessive handling and were omitted from all analyses. We assumed that no handling mortality occurred for all other bass. Only bass >200 mm TL were included in analyses because no bass under this size threshold were recaptured. In the Broad River, 200 mm is the body length that is likely to be the minimum size of bass targeted and pursued by anglers, and fish of this size are typically age 1+ based on otolith reading (J.M. Bettinger, *unpublished information*).

Capture-recapture models for closed populations infer how many more unique individuals (unobserved) should have been observed based on capture probabilities of
observed individuals. In this regard, 7,000 rows of all 0 entries were added to the data, \( y_{i,j} \), in order to represent individuals that were potentially part of the population but never observed (Royle and Dorazio 2011). The objective of capture-recapture models for abundance is then to estimate the proportion (\( \Omega \)) of individuals within this augmented data set, \( y'_{i,j} \), which should belong to the population. The following general form of capture-recapture models was fit on the augmented dataset \( y'_{i,j} \):

\[
\begin{align*}
  z_i & \sim \text{Bernoulli}(\Omega) \\
  y'_{i,j} & \sim \text{Bernoulli}(z_i \times p)
\end{align*}
\]

where \( z_i \) is the latent state of the membership in the population (\( z_i = 1 \) if a true member of the population; \( z_i = 0 \) otherwise), and \( p \) is the capture probability of individuals. Three different hypotheses of capture probability were tested: capture probability was constant over five occasions (\( M_0 \)), varied by occasion (\( M_t \)), and varied by sampling gear (\( M_g \)). Models were compared using Deviance Information Criterion (DIC) values; the model with the lowest DIC value was selected as the top-ranked model. Capture-recapture models can accommodate more complex structures such as behavior or individual variation (Otis, Burnham, White, & Anderson 1978), but convergence of these models was not achieved with our data presumably due to low recapture probabilities.

Models were analyzed through Markov-Chain Monte Carlo (MCMC) sampling methods in JAGS (Plummer 2012) called from Program R (R Development Core Team 2015). Uninformative priors were used in all models (i.e., \( \Omega \sim \text{Uniform}(0,1) \), \( p \sim \text{Uniform}(0,1) \)). Posterior distributions of parameters were estimated by keeping the
hundredth sample from 30,000 iterations of three chains after a 20,000 iteration burn-in period. Model convergence was assumed by examining plots of MCMC chains and visually ensuring mixture of all three chains. Gelman and Rubin diagnostics provided potential scale reduction factors for model parameters. Convergence of MCMC chains was assumed when values of all were parameters <1.1 (Brooks & Gelman 1998).

Model validation

The models above assume that sampling is from a single homogenous population (Otis et al. 1978). However, there was a statistically significant difference in body length between individuals captured by angling and electrofishing based on a Kolmogorov-Smirnov test (see Results). Thus, it was likely that the two gears targeted different groups of individuals (i.e., a sample of the heterogeneous population in the 4.2 km mark-recapture section). To assess model performance when the assumption of homogeneity is violated, simulations were conducted in which two groups of individuals were targeted by different sampling gears, but data from both gears were analyzed simultaneously as a single data set.

The top ranked model, M₁ (time varying; see Results), was used in simulations to investigate if known abundance can be estimated accurately. Five possible sampling scenarios were simulated, with three sampling occasions each, by varying abundance and capture probability among population segments. Abundance was set to be equal between the two segments in scenarios one and two, but the population of one segment was twice that of the other in other scenarios (Table 1-1). Abundance of each segment was set at 1000 or 2000 individuals, so that the sum of these values (2000 or 3000) was comparable to the
empirical abundance estimate obtained from the study area (see Results). Capture probability was similarly set equal in some simulations or varying in others between two segments (Table 1-1). Ranges of capture probability (10-30%) were higher than the empirical estimates (see Results), but these settings were chosen to speed computational time. A sixth scenario was also simulated, as a control, in which a single homogenous population was assumed. In all scenarios, a range of capture probabilities was specified (Table 1-1) and a capture probability was randomly drawn from the range on each sampling occasion. Each scenario was simulated 1,000 times. Distributions of posterior mean values of estimated abundance across 1,000 replicates were compared to the true known abundance, which is the sum of abundance of the two population segments. Simulations were completed using Clemson University’s Palmetto Cluster supercomputer.

Tagging & Tracking

Closed-population capture-recapture models used in this study assume no birth, death, immigration or emigration. Given the short period of time (22 days) over which mark-recapture data were collected, it was plausible that births and deaths were negligible. Assumption of no immigration and emigration was validated by tracking individuals. In May 2015, boat mounted electrofishing gear was used to collect nine bass downstream of the Ninety-Nine Islands dam, (mean: 374 mm; range: 299-476 mm TL). These fish were surgically implanted with Advance Telemetry Systems Inc. (ATS, Isanti, Minnesota) model F1580 radio transmitters. Transmitters weighed 3.6 grams in air, and the minimum (250 mm TL) tagging length was used so as not to exceed the recommended threshold of 2% of the total body mass (Winter, Kuechle, Siniff, & Tester 1978). Bass were electro-
anesthetized before surgery. After recovery in a holding tank, fish were released in slow water along the bank in close proximity (<100 m) to the point of capture.

To validate the assumption of population closure, transmitter-implanted bass were located daily during early summer (June 16-July 1, 2015). The summer tracking period (15 days) was intended to match a three-week time frame of the mark-recapture study. Mark-recapture surveys were originally planned to immediately follow daily tracking; however, timing of the two efforts did not overlap due to logistical constraints and weather events. Bass were located monthly between September 2015 and July 2016 to assess seasonal movements and identify seasons in which fish may move most and be likely to violate the closure assumption. In October, an additional five fish (mean: 436 mm; range: 365-490 mm TL) were implanted with transmitters to compensate for tag loss and increase sample size for seasonal comparisons of movement. Body size of transmitter-implanted bass did not significantly differ between May and October (t = -1.70, df = 10.60, p = 0.12).

A four-element Yagi antenna and ATS R2000 scanning receiver was used to locate transmitter-implanted fish by canoeing a 13.4 km section of the river, which included the 4.2 km mark-recapture section (Fig. 1-1). Once a strong signal was located, the coaxial cable was disconnected from the antenna. The exposed end of the cable was used to identify the locations by slowly approaching the area of the strongest signal while reducing gain (Niemela, Layzer, & Gore 1993). Where applicable, fish locations were triangulated using exposed habitat features (large boulders and exposed logs). After a transmitter location was acquired, the canoe was anchored, GPS position was noted using a handheld Dakota 10
receiver (Garmin Ltd. Olathe, KS), and water depth was measured to the nearest tenth of a meter using a wading rod (Rickly Hydological, Columbus, OH).

Movement Analyses

A total of 14 tracking events were used to calculate the daily riverine distances traveled by each bass during the 15-day summer tracking period (June 16–July 1, 2015). The riverine distances between each successive location were measured to the nearest meter for each transmitter-implanted fish to attain the minimum displacement (‘summer minimum displacement distance’ hereafter). Distances between fish locations were calculated in ArcGIS 10.3 (ESRI, Redlands, CA) using the distance along route tool based on the United States Geological Survey National Hydrography Dataset (NHDPlus V2) flowline.

Monthly minimum displacement distances were calculated as the distance traveled between two consecutive monthly tracking events, divided by the number of days between the events (Gocłowski, Kae see, & Sammons 2013). Monthly tracking intervals were grouped into four seasons based on the mean daily river temperature: summer; >20°C (June – September), fall; 20°C decreasing to 10°C (October – December), winter; <10°C (January – February), and spring; 10°C increasing to 20°C (March – May) (Todd and Rabeni 1989). River temperatures were monitored hourly in the middle of the 13.4 km telemetry section using a HOBO U22-001 data logger (Onset Computer Corp. Bourne, MA). A linear mixed effect model with random effects of transmitter-implanted bass was fit to test for
differences in minimum displacement distance among seasons (a fixed effect). Distance data were cube-root transformed prior to analysis to improve normality.

Results

Abundance estimate

A total of 468 unique individuals were captured on the five sampling occasions (141 individuals \( \leq 200 \) mm TL and 327 individuals \( >200 \) mm TL). Because the smallest recaptured individual was 208 mm TL, the analysis focused on fish \( >200 \) mm for the abundance estimate. Of the fish \( >200 \) mm, angling captured 175 unique individuals during the first two occasions, and electrofishing collected 156 unique individuals during the subsequent three occasions. Across the five total sampling occasions, one individual was captured three times, 16 individuals twice, and 331 only once. All recaptures were recorded from electrofishing surveys and no bass were recaptured on the single angling recapture occasion (i.e., the second occasion). Electrofishing captured larger bass than angling (Fig. 1-2) (a two-sample Kolmogorov-Smirnov test; \( D(352) = 0.221, p <0.0005 \)). The largest bass captured via angling was 416 mm TL, and 520 mm with electrofishing (Fig. 1-2).

The time varying model (\( M_t \)) was the top ranked of the three abundance models and no competing models were identified based on \( \Delta \text{DIC} \) values; the next supported model (\( M_0 \)) had a \( \Delta \text{DIC} = 736.77 \) relative to the top ranked model (Table 1-2). Capture probabilities differed by sampling occasion and were generally low. Mean detection probability during two angling occasions were 0.04 (4%) whereas detection probabilities during electrofishing occasions were 0.025, 0.034, and 0.013. Based on model \( M_t \), 2,380
individuals (95% CI: 1,578-3,693) >200 mm TL were estimated to be present in the 4.2 km section (Table 1-2).

Simulations

Abundance was consistently over-estimated in all five scenarios in which two different population segments were simulated but analyzed simultaneously as if they were a single sample (Fig. 1-3). Posterior mean abundance was over-estimated between 8-20% among each scenario, with the most biased estimates observed in the scenario with unequal abundance (1,000 and 2,000 individuals) and equal capture probability of both segments (0.1-0.3). The control scenario without two population segments only slightly (2%) over-estimated abundance (Table 1-1).

Bass movement

Five out of the nine initially tagged bass were available for summer daily tracking. Movement of these transmitter-implanted bass was limited during the 15-day summer tracking period. The median summer minimum displacement distance was 0.10 m (range: 0-476) (Fig. 1-4). Importantly, these five bass remained within the 4.2 km mark-recapture study section for the duration of the summer tracking period, indicating that the population closure assumption was likely met for abundance estimation.

Monthly minimum displacement distance of all bass was greatest in spring (mean = 42.62 m per day; median = 2.84 m per day), and smallest in summer by mean (20.89 m per day) and in fall by median (1.45 m per day) (Table 1-3). However, there was no significant difference in minimum displacement distance among seasons based on a linear
mixed-effects model ($p > 0.14$), due likely to large variation in movement among individuals (Table 1-3). On one hand, an individual (482 mm TL at the onset of tracking) was located within a single pool area for 12 months (Fig. 1-5). On the other hand, another individual bass (299 mm TL initially) moved 13.0 km downstream between October-November and moved back upstream 13.4 km in 36-day period (February-March) (Fig. 1-5).

**Discussion**

The dual gear sampling technique was employed in this study to accommodate varying flow conditions in a regulated river. The top-ranked abundance model ($M_t$) indicated that capture probability varied by sampling occasion and ranged between 1-4%. Varying capture probability highlighted the importance of quantifying capture efficiency for unbiased abundance estimates and lends support for field-intensive mark-recapture surveys. In the Broad River, the range of capture probabilities observed (1-4%) suggested that catch could vary four-fold depending on sampling conditions even if abundance remains unchanged.

Despite the overall success of our dual gear approach to abundance estimation, simulations suggested that our abundance estimate of bass in the Broad River was likely an over-estimate to an unknown but modest degree. Electrofishing selected for larger individuals compared to angling, which probably reflected efficiency of the former method in deeper sections of the river (Anderson 1995; Buckmeier & Schlechte 2009). In contrast, angling appeared best suited for shallower, more wadeable parts of the river. It is
reasonable to suspect that this gear bias resulted in two partially overlapping population segments, each of which was best sampled by one of the two gears used. Our scenarios simulated two completely different population segments to assess the potential extent of bias in abundance estimates. Thus, the upward bias in abundance estimate in the Broad River can be assumed smaller than those considered in the simulation scenarios (i.e., 8-20% over-estimation), although uncertainties still remain as to relative abundance of two population segments and the degree of overlap between two segments in their susceptibility to a single gear type.

Potential upward bias with the dual gear approach should not immediately discredit its application in population monitoring. Assessment of spatial and temporal trends in abundance is of great interest in fisheries management and conservation, and in the case of the Broad River, assessing a temporal trend of bass abundance to inform future stocking efforts and angler success. The trend assessment is ideally conducted with unbiased estimates; however, biased estimates could identify such trends accurately as long as the magnitude and directions of bias remain consistent (Rosenberger & Dunham 2005). In this regard, standardized sampling protocols are important in minimizing variation in bias. For example, annual sampling with the dual gear approach may employ two days of sampling with each gear to maximize the likelihood for characterizing a temporal trend of bass abundance. It is still foreseeable that a standardized sampling protocol cannot be applied consistently from year to year due to varying river conditions (i.e., only angling is possible in a drought year in the Broad River). Such additional noise would decrease statistical power to detect population trends (Dauwalter et al. 2009).
Summer daily telemetry data indicated that movement of bass was limited and population closure could be reasonably assumed for the duration of 2-3 weeks. Limited movement of smallmouth bass in rivers has been reported in summer (Langhurst & Schoenike 1990; Lyons & Kanehl 2002) and fall (Todd & Rabeni 1999). Based on monthly telemetry data, median movement distance was shortest in fall and highest in spring (Table 1-3), suggesting that the assumption of population closure may be season dependent. Thus, timing of surveys needs to be assessed when applying closed-population mark-recapture methods in rivers. When it is necessary to conduct mark-recapture in seasons when fish are likely to move farthest, studies may need to ensure population closure by other aspects of study designs such as shortening the study period and extending the study area. Seasonal telemetry data also suggested that movement distance varied by individual, with one individual documented in a local pool area for the entire 12-month duration of seasonal tracking and yet another individual moving approximately 13 km twice in two separate months (Fig. 1-5).

Estimating abundance in large water bodies such as regulated rivers and large lakes remains challenging but also provides opportunities for further studies. Standardized protocols are less common in such habitats and variable among researchers and managers (Bonar, Hubert, & Willis 2009). Efficient sampling is particularly important for mark-recapture methods. Kéry & Royle (2016) states that the first law of capture-recapture methods is that “things become more difficult when \( p \) (capture probability) gets small (p. 246)”. Improvements in analyses of abundance data are another important area for further studies and innovative approaches can lead to more accurate estimates of fish abundance.
(Korman, Schick, & Mossop 2016; Mollenhauer & Brewer 2017). Simultaneous analysis of multiple-gear data is becoming more common (Arab et al. 2008; Carrier et al. 2009), but warrants further investigations. Integrating multiple gears can be an effective and is probably a needed method for assessing abundance in spatially and temporally heterogeneous habitats.
References


fragmentation and flow regulation by global dams at multiple scales. 

*Environmental Research Letters, 10*, 015001.


Table 1-1. Six simulation settings used to assess performance of the abundance estimation model when two groups of individuals were targeted by different sampling gears, but data from both gears were analyzed as a single data set.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Abundance of each group</th>
<th>Range of capture probability for each group*</th>
<th>Posterior mean estimate of total abundance</th>
<th>Percent upward bias</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1,000/1,000</td>
<td>0.10-0.20 / 0.20-0.30</td>
<td>2,164</td>
<td>8.20</td>
</tr>
<tr>
<td>B</td>
<td>1,000/1,000</td>
<td>0.10-0.30 / 0.10-0.30</td>
<td>2,364</td>
<td>18.20</td>
</tr>
<tr>
<td>C</td>
<td>1,000/2,000</td>
<td>0.10-0.30 / 0.10-0.30</td>
<td>3,609</td>
<td>20.30</td>
</tr>
<tr>
<td>D</td>
<td>1,000/2,000</td>
<td>0.10-0.20 / 0.20-0.30</td>
<td>3,268</td>
<td>8.93</td>
</tr>
<tr>
<td>E</td>
<td>1,000/2,000</td>
<td>0.20-0.30 / 0.10-0.20</td>
<td>3,422</td>
<td>14.06</td>
</tr>
<tr>
<td>F</td>
<td>3,000**</td>
<td>0.20-0.30</td>
<td>3,068</td>
<td>2.26</td>
</tr>
</tbody>
</table>

*For each iteration, capture probabilities were randomly drawn from a uniform distribution.

**Control assuming a single population segment.
Table 1-2. Estimated abundance of smallmouth bass, and Bayesian DIC rankings of three models to estimate smallmouth bass abundance in a 4.2-km section of the Broad River.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate (95% CI)</th>
<th>DIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_t$</td>
<td>2,380 (1,578-3,693)</td>
<td>14,495.86</td>
</tr>
<tr>
<td>$M_0$</td>
<td>2,933 (1,868-3,264)</td>
<td>15,232.63</td>
</tr>
<tr>
<td>$M_g$</td>
<td>2,792 (1,755-4,520)</td>
<td>17,849.65</td>
</tr>
</tbody>
</table>

Table 1-3. Mean, median, and range of monthly minimum displacement distances (m) and overall number of smallmouth bass tracked within each season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Mean</th>
<th>Median</th>
<th>Min</th>
<th>Max</th>
<th>No. of fish located</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer 2015</td>
<td>20.89</td>
<td>2.46</td>
<td>0.00</td>
<td>238.29</td>
<td>9</td>
</tr>
<tr>
<td>Fall 2015</td>
<td>24.98</td>
<td>1.45</td>
<td>0.03</td>
<td>422.03</td>
<td>12</td>
</tr>
<tr>
<td>Winter 2015-16</td>
<td>31.27</td>
<td>2.08</td>
<td>0.02</td>
<td>380.69</td>
<td>12</td>
</tr>
<tr>
<td>Spring 2016</td>
<td>42.62</td>
<td>2.84</td>
<td>0.05</td>
<td>380.69</td>
<td>12</td>
</tr>
</tbody>
</table>
Figure 1-1. Major rivers of South Carolina with expanded study area of the Broad River between Ninety-Nine Islands and Lockhart Dams depicting the upper mark-recapture section (4.2 km) within the radio tracking reach (13.4 km). The river flows from the north to the south.
Figure 1-2. Length frequency histograms of all bass captured using angling (A) and electrofishing (B).
Figure 1-3. Distributions of posterior means of 1000 replicate simulations of the time varying, Mt, models for six different scenarios: (A) Equal detection of two equal population segments of 1000 individual fish each. (B) Unequal detection of two equal size segments of the population. (C) Equal detection of unequal size segments of the population. (D) Larger detection of a larger segment of the population. (E) Larger detection of a smaller segment of the population. (F) A control simulation estimating a single population size of 3000 individuals (F). See Table 1-1 for a detailed description of each scenario. Dashed vertical lines indicate the true total abundance.
Figure 1-4. Locations of five smallmouth bass tracked daily with radio telemetry below the Ninety-Nine Islands Dam tailrace between June 16 and July 1, 2015. Different symbols indicate different individuals. Perpendicular lines crossing river channel designate boundaries of large shoals.
Figure 1-5. Monthly locations of four transmitter-implanted smallmouth bass that survived for 12 months of the study. Perpendicular lines crossing river channel designate boundaries of large shoals.
CHAPTER TWO

Power analysis of mark-recapture population monitoring designs to detect a temporal decline in smallmouth bass abundance.

Introduction

Long-term population monitoring informs fisheries management. Identifying a temporal trend in abundance is a vital goal in many federal and state agencies’ management programs (Butowski & Morin 2016). This information can be used to establish creel limits, evaluate angler exploitation (Beard et al. 1997; Sullivan 2003) and assess the need for stocking (Post 2013). Thus, it is imperative to ensure that a population trend is readily detected over time (Dauwalter et al. 2009).

The statistical power (1 – β, where β is the probability of type II error) to detect such trends in abundance is influenced by a multitude of factors such as precision of abundance estimates, the sample sizes obtained (Gerow 2007), temporal fluctuations in population size, and the amount of harvest (Peterman 1990). With additional data, declines within a certain area could be linked to causes of declines such as disease (Lafferty & Holt 2003), and changes in water quality (McClelland et al. 2012).

The amount of resources (i.e. equipment, workers, and time) devoted to a fish population survey will affect the ability to accurately estimate population size. These costs of sampling will often constrain the ability to effectively monitor fish populations (Possingham et al. 2001) and sampling designs dictated by resource/cost constraints can affect our ability to detect a temporal trend (Urquhart & Kincaid 1999). Identifying an
optimal long-term population monitoring plan which incorporates constraining factors (e.g. inter-annual changes in crew size, availability of sampling equipment, fuel costs, etc.) is important for maximizing the effectiveness of a long-term monitoring strategy (Hauser et al. 2006; Marsh and Trenham 2008). When creating an effective monitoring program, it is integral to identify the point at which using additional resources may no longer improve estimates and produce only minimal gains in the precision and accuracy of population estimates through time (Bailey and Gerow 2005; Gwinn et al. 2011).

The objective of this chapter is to compare the power to detect temporal population declines using the population estimation model developed in chapter 1. Specifically, I simulated 2.5% and 5% annual declines in Broad River smallmouth bass abundance and compared statistical power to detect the declines by nine different sampling scenarios of varying sampling efforts after 5, 10 and 15 years. This power analysis was intended to help inform the South Carolina Department of Natural Resources on the most appropriate allocation of limited resources to monitor smallmouth bass abundance in the Broad River over time.

**Methods**

Nine sampling plans of varying effort were considered in the simulation and their statistical power to detect a population decline was quantified. The initial bass abundance was set at 2,500 individuals which corresponded to the empirical abundance estimate of smallmouth bass (>200mm TL) obtained in chapter 1. Two annual population decline trends (2.5% and 5%) were simulated, and fish sampling and abundance estimation was
assumed to take place under the initial condition (current year) and then at five-year intervals (i.e., 5, 10 and 15 years).

The top empirical Broad River smallmouth bass mark-recapture model (M_t) was used in this simulation study where an augmented dataset of captured bass was used to estimate annual abundance (see chapter 1). The model is described as:

\[ z_i \sim \text{Bernoulli}(\Omega) \]

\[ y'_{i,j} \sim \text{Bernoulli}(z_i * p_t) \]

where \( z_i \) is the latent state of the membership of individual \( i \) in the population (\( z_i = 1 \) if a true member of the population; \( z_i = 0 \) otherwise), and \( p_t \) is the detection probability of individual bass on sampling occasion \( t \).

I considered that those who would implement this model could control sampling effort in two ways. Specifically, one can control the number of sampling occasions per year (‘annual effort’ hereafter) and the number of electrofishing boats per occasion which would affect capture probability of individuals (‘occasion effort’ hereafter). Thus, three levels of effort (low, medium and high) were simulated for both annual and occasion effort, resulting in nine (3×3) different sampling protocols.

For annual effort, three levels corresponded to 3, 5 and 7 sampling occasions per year (Table 2-1). The low effort (3 occasions annually) was the minimum number needed to adequately estimate abundance using the closed-population approach (Otis et al. 1978), and effort was increased by two additional occasions for the medium and highest levels.
For occasion effort, three levels corresponded to capture probability \( p \) equal to 3-8\% (low effort), 8-13\% (medium) and 13-18\% (high). The low effort was intended to represent sampling using a single electrofishing boat; this was the sampling method used in my fieldwork and mean capture probability of individuals was 4\% across three electrofishing occasions (chapter 1). However, more than one electrofishing boat can sample the study area simultaneously and up to five boats were operated at the same time in a pilot study conducted in Broad River. Assuming that detection would be additive based on the number of electrofishing boats, the medium effort was set at 8-13\% (2 to 3 boats) and 13-18\% (4 to 5 boats). In simulations, detection probability for each sampling occasion was derived by a random draw from a uniform distribution given the range specified for each effort level. All simulations were performed on Clemson University’s Palmetto Cluster supercomputer and each of the nine sampling plans was simulated 500 times.

Statistical power to detect a temporal decline was assessed by comparing initial abundance to that in years 5, 10, and 15 using Bayesian one-tailed t-tests (Kery 2010) and three different significance levels \( \alpha = 0.05, 0.15, \) and 0.25. Specifically, statistical significance was declared in each iteration by comparing posterior abundance values between the initial year and each successive sampling interval \( \Delta = \text{abundance in the initial year} - \text{abundance in a subsequent year} \). For example, using \( \alpha = 0.05 \), a temporal decline was considered to be detected when >95\% of \( \Delta \) values were negative. Statistical power of each sampling plan was then the proportion of statistically significant iterations among the 500 individual runs.
Results

Increasing sampling effort resulted in less biased (Fig. 2-1a) and more precise (Fig. 2-1b) abundance estimates. Higher occasion effort (i.e. higher detection probability) and annual effort (i.e. more sampling occasions per year) led to posterior mean estimates consistent with the simulated abundance value of 2,500 individuals (Fig. 2-1a). Precision similarly increased with higher occasion and annual effort (Fig. 2-1b). However, posterior 95% CI of abundance estimates were wide. Even in the high occasion and high annual simulation, 95% CI of abundance covered a range of 2195 - 2770 individuals (Fig. 2-1b), which would decrease statistical power to detect a temporal trend.

Not surprisingly, statistical power to detect a trend increased with sampling effort, as well as years passed between samples, the severity of annual decline and increasing $\alpha$ levels (Fig. 2-2 & 2-3). Most importantly, occasion effort (detection probability per occasion) was more influential than annual effort (number of sampling occasions per year) in affecting statistical power. In both 2.5% (Fig. 2-2) and 5% (Fig. 2-3) scenarios of annual decline, simulations with high detection probability resulted in power >0.95 regardless of number of occasions per year (annual effort) and the number of sampling years passed. Power declined as detection probability decreased. For example, in simulations assuming three sampling occasions per year, 2.5% annual decline and $\alpha = 0.05$, power was 1.00 with high detection, 0.32 with medium detection and 0.07 with low detection (Fig. 2-2).

The number of years passed between samples was another key driver of statistical power. After 15 years, power to detect a trend was high ranging from 0.65-1.00 with many
scenarios achieving power of 1.00 (Table 2-1). However, power varied with smaller numbers of years between samples, particularly after 5 years (Fig. 2-2 & 2-3). In other words, sampling designs were crucial when attempting to detect a temporal trend over a short period, but were less important for trend detection over a long period.

Finally, relaxing $\alpha$ levels increased power (Fig. 2-2 & 2-3). For example, in the scenario with a 2.5% annual decline, 3 sampling occasions annually, and medium detection probability, power to detect a trend after 10 years increased from 0.51 with $\alpha = 0.05$ to 0.70 ($\alpha = 0.15$) and 0.78 ($\alpha = 0.25$) (Table 2-1; Fig. 2-2).

**Discussion**

Statistical power to detect trends increased with sampling effort. A notable finding of the simulations was that occasion effort (detection probability) was more important than annual effort (number of sampling occasions annually) in influencing statistical power. That is, high detection ensured high power in all scenarios considered in this chapter. I propose that this result was due to the low overall detection probability levels used in the simulations. Kéry & Royle (2016) stated that the first law of capture-recapture methods was that “things become more difficult when $p$ (capture probability) gets small (p. 246)”.

The mean empirical estimate of detection probability was 4% for smallmouth bass in Broad River (chapter 1) and our three detection probabilities were set at 3-8 % (low), 8-13 % (medium) and 13-18 % (high). In one sense, the low detection probability was a ‘limiting factor’ in abundance estimates and simulations (Chapter 1), and increasing this value even slightly should aid in deriving less biased and more precise estimates of abundance, which
would then increase statistical power. In the meantime, three occasions (low annual effort) are frequently used in occupancy and abundance estimation for closed populations (MacKenzie et al. 2002; Royle 2004). While increasing number of sampling occasions should increase statistical power, the range of annual effort settings was likely not as ‘limiting’ as detection probabilities. Based on the simulations, I recommend that future monitoring effort prioritize maximizing occasional effort over annual effort. In other words, high detection probability (e.g. using multiple electrofishing boats) should be prioritized with a trade-off of fewer sampling occasions annually.

Our results of higher power with increasing sampling effort are in concordance with previous studies of power analyses. Power of trend detection typically increases with number of annual samples and rate of annual decline (Ham and Pearsons 2000; Dauwalter et al. 2009; Russell et al. 2012). It is important to note that sampling designs mattered most when attempting to detect a short-term decline (i.e., after 5 years) in this study, and once again occasion effort was more important than annual effort in achieving high statistical power.

Although detecting a trend over a short period is typically challenging (Dauwalter et al. 2009; Russell et al. 2012), this could be overcome by relaxing α levels at the cost of being prone to more likely committing type I errors (i.e. falsely identifying a trend when such a trend does not truly exist). Three different α levels (0.05, 0.15 & 0.25) were used in this study using a Bayesian approach, which indicated that one would be 95%, 85% & 75% confident that a negative trend existed given the data. Thus, it was no surprise that relaxing α levels (i.e. lowering the threshold for trend detection) resulted in higher statistical power.
Statistical significance is typically set at $\alpha = 0.05$, but this threshold should be evaluated case-by-case based on management actions and implications. In maintaining a recreational fishery of smallmouth bass in the Broad River, falsely identifying a negative trend using relaxed $\alpha$ levels could trigger management actions such as stocking or fishing restrictions earlier than they should occur. However, this type of error would not further jeopardize fisheries resources (the error here is that fisheries resources are protected too early). Statistical significance ($\alpha$ levels) should be carefully examined particularly when the goal of the monitoring plan is to detect a short-term trend.

One caveat of the simulation approach in this study was that temporal variation in abundance was not accounted for. Population abundance naturally fluctuates over time and the magnitude of the temporal variation is large in many populations of freshwater fishes (Stevens et al. 1985; Gibbs 2000; Rose 2000; Dauwalter et al. 2009). This temporal fluctuation functions as a ‘noise’ to blur the temporal pattern, thus negatively affecting power to detect a temporal trend. Given the lack of long-term monitoring data of smallmouth bass in Broad River, temporal variation in abundance could not be quantified and incorporated in the simulations. This means that power in my simulations represents the most optimistic level, and would be lower to an unknown degree if temporal noise had been present. Still, the major conclusions about sampling designs (e.g. occasional effort is more important than annual effort) should hold true and due consideration should be given when drafting a monitoring plan for detecting smallmouth bass abundance trend in the Broad River.
References


Table 2-1.

Statistical power to detect a 2.5 and 5% annual decline in a smallmouth bass population at significance levels ($\alpha$) = 0.05, 0.15, and 0.25 under nine possible simulation scenarios. Years passed between sampling events are shown by t+5 (5 years later), t+10 (10 years later) and t+15 (15 years later).

<table>
<thead>
<tr>
<th>Sampling Occasions</th>
<th>Detection Probability</th>
<th>Annual Decline</th>
<th>Annual Effort</th>
<th>Occasion Effort</th>
<th>Power ($\alpha = 0.05$)</th>
<th>Power ($\alpha = 0.15$)</th>
<th>Power ($\alpha = 0.25$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>3-8%</td>
<td>2.5%</td>
<td>Low</td>
<td>Low</td>
<td>0.07 0.12 0.65</td>
<td>0.24 0.39 0.81</td>
<td>0.40 0.61 0.88</td>
</tr>
<tr>
<td>3</td>
<td>8-13%</td>
<td>2.5%</td>
<td>Low</td>
<td>Medium</td>
<td>0.32 0.51 0.65</td>
<td>0.58 0.70 0.99</td>
<td>0.74 0.78 1.00</td>
</tr>
<tr>
<td>3</td>
<td>13-18%</td>
<td>2.5%</td>
<td>Low</td>
<td>High</td>
<td>1.00 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
</tr>
<tr>
<td>5</td>
<td>3-8%</td>
<td>2.5%</td>
<td>Medium</td>
<td>Low</td>
<td>0.01 0.61 1.00</td>
<td>0.06 0.89 1.00</td>
<td>0.19 0.96 1.00</td>
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<tr>
<td>5</td>
<td>8-13%</td>
<td>2.5%</td>
<td>Medium</td>
<td>Medium</td>
<td>0.91 1.00 1.00</td>
<td>0.97 1.00 1.00</td>
<td>0.99 1.00 1.00</td>
</tr>
<tr>
<td>5</td>
<td>13-18%</td>
<td>2.5%</td>
<td>Medium</td>
<td>High</td>
<td>0.96 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
</tr>
<tr>
<td>7</td>
<td>3-8%</td>
<td>2.5%</td>
<td>High</td>
<td>Low</td>
<td>0.87 1.00 1.00</td>
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<tr>
<td>7</td>
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<td>2.5%</td>
<td>High</td>
<td>Medium</td>
<td>0.86 1.00 1.00</td>
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<tr>
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<td>2.5%</td>
<td>High</td>
<td>High</td>
<td>1.00 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
<td>1.00 1.00 1.00</td>
</tr>
<tr>
<td>3</td>
<td>3-8%</td>
<td>5%</td>
<td>Low</td>
<td>Low</td>
<td>0.02 0.62 0.86</td>
<td>0.10 0.80 0.91</td>
<td>0.20 0.88 0.93</td>
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<tr>
<td></td>
<td>8-13%</td>
<td>5%</td>
<td>Low</td>
<td>Medium</td>
<td>0.32</td>
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</tr>
<tr>
<td>3</td>
<td>13-18%</td>
<td>5%</td>
<td>Low</td>
<td>High</td>
<td>1.00</td>
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<td>1.00</td>
</tr>
<tr>
<td>5</td>
<td>3-8%</td>
<td>5%</td>
<td>Medium</td>
<td>Low</td>
<td>0.47</td>
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<td>8-13%</td>
<td>5%</td>
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<td>Medium</td>
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<tr>
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<td>High</td>
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</table>
Figure 2-1. Distributions of posterior means (A) and 95% credible intervals (B) across 500 iterations for nine simulation scenarios of varying combinations of occasion and annual sampling effort levels. Dots indicate mean values and ranges are 95% quantiles. Dashed line indicates the simulated abundance of 2500 individuals.
Figure 2-2. Statistical power to detect a 2.5% annual decline at significance (α) levels = 0.05, 0.15, and 0.25 under nine variants of sampling designs. Sampling was simulated under three different levels of occasions per sampling year with three levels of individual bass detection per occasion.
Figure 2-3. Statistical power to detect a 5% annual decline at significance (α) levels = 0.05, 0.15, and 0.25 under nine variants of sampling designs. Sampling was simulated under three different levels of occasions per sampling year with three levels of individual bass detection per occasion.
CHAPTER THREE

Influence of discharge on diurnal movement of smallmouth bass:

A time series analysis of fish movement.

Introduction

The flow regime is a major driver of the function and productivity of the river system. Riverine species have adapted to specific flow regimes, and alterations of the natural flow patterns can result in more frequent changes in the magnitude of both high and low river flow (Poff et al. 1997). Changes to the natural flow regime include dam releases and water management practices which influence fish populations and behavior in both positive and negative ways (Taylor & Cooke 2012). Flow alterations due to dams and channelization can lead to ecological changes throughout the entire river system, and affect fish abundance, community structures, and individual feeding behaviors (Lagarrigue et al. 2002; Osmundson, Ryel, Lamarra, & Pitlick 2002; Haxton & Findlay 2008).

Species specific studies have produced understandings into the influence of hydrological modifications on fish distributions through time (Earley 2012). Natural flooding events influence fish movement in the seeking of flow refugia (David & Closs 2002), but artificial fluctuations in river flow (i.e. dam releases and lack thereof) can also affect movement patterns (Armstrong, Braithwaite, & Fox 1998). There are different levels of flow modification which may influence the movements of fish through time. For example, peaking hydropower generation can cause very large and rapid changes in flow,
or decreased releases from water control structures can lead to diminished base flow during drought conditions.

Dam releases and flow regime fluctuations produce variations in river discharge that can influence both the timing and length of long-distance migrations (i.e. spawning runs) (Miller & Scarnecchia 2008), and also impact behavior over much shorter time scales (Poff & Zimmerman 2010). It is the shorter-term variations in discharge (those changes which occur over a period of hours) (Miller & Scarnecchia 2008) that can affect non-migratory fish movement (the daily activities that are not associated with spawning or seasonal changes) (Taylor & Cooke 2012). If these short-term temporal changes in discharge influence fish movement, then it is important to assess the impact of the short-term variations in discharge on non-migratory movement. Frequent changes in river discharge have short-term effects on feeding frequency (Snedden, Kelso, & Rutherford 1999) and foraging patterns (Bartumeus, da Luz, Viswanathan, & Catalan 2005). Frequent high discharge increases energetic costs of feeding which can reduce fish growth rates (Paragamian & Wiley 1987; Zorn & Seelbach 1995). Discharge acting as such a ‘stressor’ can then lead to subsequent population level effects through reduced body growth and survival (Hunter 1992; Taylor & Cooke 2012).

Non-migratory fish movements are often regarded as an indicator of habitat preferences or selection of different areas which have more favorable conditions (i.e. moving from a riffle to a pool with deeper water) (Bolland, Cowx, & Lucas 2008). River discharge fluctuations could act as an additional factor affecting behavior, resulting in more or less movement than during periods with stable flow patterns. The additional indirect
impact could then be that short-term fluctuations of discharge further stimulate movement in addition to the behavior of simply selecting different habitats (Hunter 1992). Habitat selection is an important objective of studying fish movement, but it is also important to quantify environmental drivers that may influence the behavior of fish in altered habitats such as regulated rivers (Facey & Grossman 1992).

Here, we consider the effect of river discharge on fine-scale diurnal fish movement by following single bass throughout an entire daylight period. Hourly changes in discharge are common in this study area of the Broad River as electricity is generated at the Ninety-Nine Islands Hydroelectric Station (see Fig. 1-1 of Chapter 1). Specifically, the Ninety-Nine Islands Hydroelectric station is a hydropower dam which impounds a small reservoir of 358 hectares and produces flow alterations with various magnitudes throughout the year. Potentially negative effects of hydropower generation on bass movement could affect bass populations that support a sizeable recreational fishery in the Broad River. Thus, this study would provide key information on balancing power generation and fisheries conservation. Using regression analysis, I report that bass movement and discharge were weakly correlated in winter, but not in summer.
Methods

Tracking

I investigated diurnal movement of the radio-tagged smallmouth bass by locating them every 30 minutes for an entire daylight period. Six radio-tagged bass (mean: 414 mm TL; range: 299-490) were tracked up to a maximum of 1 km downstream of the Ninety-Nine Islands dam (Fig. 1-1 of Chapter 1). Bass were located using the same zero-point gain reduction telemetry methods as previously described in Chapter 1 (Nimela et al. 1993). Bass were tracked during two seasons, summer (July and August) and winter (December-February). In summer, individual bass were tracked over the course of two consecutive days where individual fish point locations were recorded from 6:30a.m.-2:00 p.m. on the first day and 2:00 p.m.-9:00 p.m. on the second. During winter, shorter photoperiods allowed for fish to be followed during a single day long period (7:00a.m. – 6:00p.m.).

Once a bass was relocated, water depth was measured to the nearest tenth of a meter using a wading rod (Rickly Hydrological Co., Columbus, OH) and the point location was recorded using a Garmin Dakota 10 receiver (Olathe, KS). A total of 392 bass relocations were obtained on 26 individual tracking days (20 during summer and six during winter). Bass movement between consecutively recorded distances was computed by measuring the straight-line distances using ArcGIS 10.3 (ESRI, Redlands, CA). Lateral movement was treated the same as up/down stream directions. Thus, a change in any direction within the river channel was simply considered a linear movement.

Statistical Analyses
To examine day-time movement of bass in response to changes in discharge, movement distances were analyzed in regression analyses using all individuals simultaneously. The primary interest lied in understanding the overall patterns of bass movement in relation to discharge fluctuation while accounting for individual differences. While the main objective was to investigate the effects of discharge on bass movement, seven other variables that were hypothesized to affect bass movement were considered: water depth, period of daylight (twilight: prior to 6:30a.m./after 9:00 p.m. during summer, prior to 6:30 a.m./after 7:00p.m during winter; dawn: 6:30-7:00a.m. during summer, 7:00-7:30a.m. during winter; morning: 8:00-11:30a.m., afternoon: 12:00-5:00p.m, evening: 5:00-8:30p.m. during summer, 5:00-6:30p.m. during winter, and dusk 8:30-9:00p.m. during summer, 6:30-7:00p.m. during winter), river discharge, difference in discharge from the previous detection ($\Delta$Discharge = Discharge$_t$ – Discharge$_{t-1}$), percent change in discharge from the previous detection ($\%\Delta$Discharge = $\Delta$Discharge / Discharge$_{t-1}$*100), and body size (total length in mm). Discharge data was obtained from USGS Gage 02153551. Period of day and fish size were included since they can influence bass activity (Reynolds & Casterlin 1976; Todd & Rabeni 1989). Both summer and winter data was first analyzed together as a global model. However, due to drought conditions during summer and increased precipitation during winter, summer and winter discharge levels differed greatly: winter median discharge during tracking dates (3070 ft.$^3$/sec.) was much higher than that of summer (576 ft.$^3$/sec.). To remove a potentially confounding effect of season, summer and winter were analyzed independently. On a few occasions during summer tracking, tagged bass had seemed to move with increasing discharge levels, thus I
hypothesized that fish movement distances would be positively correlated with increases in river discharge.

*Model development*

I used a two-step approach to quantify the effect of discharge on daylight bass movement within summer and winter seasons. Since bass movements did not reflect an obvious linear trend in response to discharge levels, I implemented Generalized Additive Mixed Models (GAMMs) to accommodate the non-linear responses. First, models were developed with individuals as a random effect and were used to address bass movement with variation in river discharge levels over time. Temporal correlation structure in recorded bass locations was not yet accounted for in the first step, before model development, I used variance inflation factors (VIF) to assess collinearity between the predictor variables. All variables had a VIF value less than three and were retained for further model development (Zuur *et al.* 2009). GAMMs were employed using package mgcv (Wood 2006) in Program R and a cubic regression spline was applied, allowing for a non-linear curve based on smother regression (Zuur *et al.* 2009). Initially, smoothing terms were added to all variables, but were removed from bass body size which did not have enough unique values to include as a smoother (Zuur *et al.* 2009). The optimal set of covariates to be included in the subsequent time-series analysis was selected by dropping non-significant covariates until all remaining covariates were significant ($\alpha \leq 0.05$).

*Time Series Analysis*
Since movement data were essentially a time series of individual movement events, the second step in the regression analysis was to add a correlation structure to the optimal GAMMs to account for the possibility of serial autocorrelation of the tracking observations through time. Final time series GAMMs used the optimal set of predictor variables identified above and the correlation structure observed in their residual plots. To accomplish this, the correlation lag structure of residuals was visually evaluated for the top initial GAMMs. Based on the significant partial autocorrelations at lags one and four (Figs. 3-1), and AR-1 and ARMA(4,1) were fit to summer movement. Winter showed an oscillating autocorrelation, a significant lag-1 partial autocorrelation, and a significant lag six autocorrelation; an ARMA(2,1) and MA(6) model structure was fit to winter data in an attempt to account for these lag cycles (Fig. 3-2). To select the best fitting of the time series correlation structures, Akaike information criterion (AIC) was used to rank each model for each season and the model with the lowest AIC score for each season was considered the top model. No competing models were identified based on ΔAIC rankings (ΔAIC >2 from the top-ranked model).

**Results**

The mean consecutive (30 minute interval) distance traveled by all of the bass during both seasons was 30 m. Summer mean distance was 31 m (range: 2-172 m) and winter was comparable with a mean of 26 m (range: 1-170 m). Median movement was 22 m in summer and 15 m in winter. Movement distances did not differ significantly by season (Kolmogorov-Smirnov Test; $D = 0.19$, $p = 0.01$). All bass that were tracked remained within pool/run habitats ($<1000 \text{ m}^2$) during a single diurnal tracking period.
Discharge Predictor variables retained in the final GAMMs included discharge, water depth, and bass total length as the optimal parameter set to use for time series analyses. Period of day was not significant during model development, and was thus dropped prior to time series AIC rankings. Absolute discharge was the only significant discharge variable in the final set of time series models (Table 3-1). Discharge was not significant for summer \((p = 0.51)\), but was significant in winter \((p = 0.04)\). The final time series GAMM for both seasons incorporated two different correlation structures based on the lag significances seen in the autocorrelation plots (Figs. 3-1 & 3-2). The top time series models were as follows:

Summer:

\[
\text{Movement}_{i,t} = s(\text{Depth}_t) + \text{Body Size}_i + \text{CorARMA}(\phi_i - \theta_{i,t-1})
\]

Winter:

\[
\text{Movement}_{i,t} = s(\text{Discharge}_t) + \text{Body Size}_i + \text{CorARMA}(\theta_{i,t-6})
\]

Where movement of individual \(i\) at time \((t)\) is influenced by \(\phi\), the \(t - t-t\) (lag) difference in observations and \(\varepsilon_{i,t-1}\) (the lag difference in errors and random effect of individual bass) correlation structures observed in the residual plots for the summer and winter models respectively, and cubic regression shrinking terms (denoted by the letter ’s’) were included on discharge and depth variables.

For summer, the final time series model indicated that bass movement increased slightly more at both shallower and deeper depths. Depth was however weakly correlated
with bass movement ($F = 0.041, p = 0.058$) (Fig. 3-3). The curvilinear relationship between summer depth and the influence on movement during summer indicated slightly more movement at both higher and lower than average discharge levels (Fig. 3-3).

The top winter time series GAMM showed that movement exhibited a linear positive trend with increasing discharge levels (Fig. 3-4). The winter analysis showed that movement was correlated with both discharge ($F = 4.226, p = 0.042$) and depth ($F = 0.031, p = 0.050$) (Fig. 3-4). Body size of the bass was significantly positive for the winter series only (summer: $p = 0.160$; winter: $p = 0.020$).

**Discussion**

Taylor & Cooke (2012) report that non-migratory fish movements increased with changes in river discharge. My investigation of the effects of river discharge on smallmouth bass movement also support this general trend discovered in their meta-analysis, although correlation was weak in my study ($R^2 = 0.04$ for summer and 0.03 for winter). Correlation was slightly stronger in winter most likely due to the increased discharge levels during that season. The positive relationship seen for winter discharge (Fig. 3-4) indicated that movement was influenced more during a period of higher discharge from the dam. The increased response during winter can be attributed to a physiological response where fish are likely seeking areas with lower flows to save energy and lessen the costs of swimming (Flore & Keckeis 1998), especially during times with the coldest water temperatures ($< 20^\circ C$).
Bass response to changing flows is also noted by summer depths. Smallmouth bass exhibited longer movements when location depths were less than 0.4 m or greater than 1.2 m (i.e. bass are more likely to move under higher flow conditions versus more stable base levels) (Fig. 3-3). This type of movement pattern at the lowest discharges points toward a lack of water available within the channel (Fig. 3-5a), but more movement during the highest discharges and water levels lends to the growing knowledge of the effects of peaking power generation discharge levels on black bass movement (Earley 2012) where bass could be seeking flow refuge (Sammons & Earley 2015). Or, fish could perhaps be moving toward areas of higher flow for additional feeding opportunities. Higher flows could cause substrate disturbance and thus feeding opportunities (Kemp, Gilvear, & Armstrong 2006). The latter is probably less plausible, but a diet study of stomach contents taken from bass after above average discharge events could bring insights into which exact behavior may be happening during highest magnitude flows (Valentine, Sabaton, Breil, & Souchon 1996).

Studying fish movement in relation to varying discharge levels over a short time period (within a single day) allowed me to quantify fine-scale behavior of smallmouth bass over time. Night tracking to obtain an entire diel period would have been ideal in the investigation of how Broad River smallmouth respond to discharge changes (Todd & Rabeni 1989), but tracking at night was not safe due to the numerous exposed shoals within the river channel in Broad River.

Assuming that lower peak flows could result in easier feeding opportunities for individual fish, managing discharge in an optimal ‘feeding range’ could be an important
tactic for Broad River fishery managers to work with dam operators in order to maximize individual bass growth and angler satisfaction. Managing a regulated river for both power generation and a productive fishery is a daunting task, but could result in an optimal situation for both power generation and non-consumptive uses such as sport fishing (Gore & Petts 1989). Repeated hydraulic stress could create diminished fish conditions and hinder population growth rates as a result (Earley 2012). More data at the extreme discharge levels (e.g. those time periods when river discharge is $<400$ and $>5000$ ft$^3$/sec. in this reach), is needed to completely parse out the nuances of how discharge affects top predator physiology and behavior. More effort is also needed to scale individual-level movement responses to discharge to population-level effects (Taylor & Cooke 2012).

These data do not support a strong effect of discharge on bass behavior. Here, smallmouth bass movement was influenced by increased discharge, and based on this analysis of discharge and depth, there is limited evidence to support the influence of both lower and higher discharge events on the overall pattern of bass movement in response to changing river conditions (Fig. 3-4). With additional efforts to quantify the impact of flow regulation on the physiological responses of highly active predators like smallmouth bass, we could consider new regulations that will benefit below-dam fish communities as a whole (i.e. both the specialized and generalist species) (Poff & Zimmerman 2010). Hydropower generation should remain a priority, but also maintaining fish communities should enhance angler opportunities by maximizing the invertebrate abundance and the overall food web structure (Malmqvist 2002).
It is also important to note that in many places outside of the native range, smallmouth bass have become a naturalized top predator (Brewer & Orth 2015) which may be able to exploit optimal conditions and maximize population growth. Management practices which maximize population growth would need to have monitoring protocols (see Chapters 1 & 2) to either ensure a minimum impact on native species (Zimmerman 1999), or maximize bass recruitment for the sport fishery (Smith et al. 2005; Zipkin et al. 2008) depending on specific management goals.
References


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*Ecology of Freshwater Fish, 15*, 565-571.


Zimmerman, M. P. (1999). Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile
anadromous salmonids. Transactions of the American Fisheries Society, 128, 1036-1054.


Table 3-1. Summary Statistics, significance of variables, and AIC values for each time series correlation model fit to summer and winter bass movement data.

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<th>Model</th>
<th>$R^2$</th>
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<th>$p$-value</th>
<th>Period of Day</th>
<th>%ΔDischarge</th>
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Figure 3-1. Autocorrelation plots of summer movement GAMM normalized residuals correlation lag structure.
Figure 3-2. Autocorrelation plots of winter movement GAMM normalized residuals correlation lag structure.
Figure 3-3. Estimated influence of log$_{10}$ transformed summer depth (m) and bass total length (mm) on diurnal bass movement based on the summer time series GAM. Approximate 95% pointwise confidence intervals are given by the dashed lines. Depth influence is scaled and mean-centered. River Discharge was not significant in the model.
Figure 3-4. Estimated influence of $\log_{10}$ transformed winter discharge (ft.$^3$/sec.), depth (m), and bass total length (mm) on diurnal bass movement based on the summer time series GAM. Approximate 95% pointwise confidence intervals are given by the dotted lines. Discharge and depth influence is scaled and mean-centered.
Figure 3-5. Photos of the Ninety-Nine Islands tailrace during low discharge (A) and high discharge (B) conditions.